NEW TAXA IN *OENOTHERA* (ONAGRACEAE)[1]

WARREN L. WAGNER[2]

ABSTRACT

A new species, three new sections, and one new subsection of *Oenothera* are described and a new combination in *O. flava* is made here so that the names will be available. **Oenothera coryi** (sect. *Megapterium*), which ranges from north-central Texas to the southern part of the panhandle, is described. The combination *O. flava* subsp. *taraxacoides* (sect. *Lavauxia*) is made for large-flowered, modally outcrossing populations of *O. flava* from three disjunct areas: 1) Mogollon Plateau, Arizona to Catron Co., New Mexico; 2) Sacramento Mountains and Sierra Blanca in southeastern New Mexico; and 3) Sierra Madre Occidental from Chihuahua to Durango, Mexico. As part of a genus-wide re-evaluation of the infrageneric classification, three new sections, **sect. Ravenia, sect. Eremia,** and **sect. Contortae,** are proposed for species formerly included in subg. *Pachylophus,* which is no longer recognized, and **subsect. Australis** is described for the two white-flowered South American species of sect. *Lavauxia.*

A number of concurrent studies of *Oenothera* are in progress, including studies of flavonoids, seed anatomy and morphology, and pollen morphology. Several new names are published here in order to make them available prior to the publication of detailed revisions of the sections in which they occur. With the publication of this paper and an upcoming paper on the systematics of subsect. *Raimannia* and a related new subsection (Dietrich et al., submitted) all taxa in the genus will have been published that have been recognized in a series of detailed systematic studies initiated in the mid-1960s by Peter Raven. Detailed discussion of the new taxa and one combination presented here will be made in the respective sectional revisions.

OENOTHERA SECT. *MEGAPTERIUM*

This section consists of four species. The most distinctive is *Oenothera macrocarpa* Nutt., a polymorphic species of the Great Plains that is subdivided into four subspecies (Wagner, 1983). The other three species were previously included by Munz (1930) in *O. brachycarpa* A. Gray. Detailed study of morphology, cytology, and distribution showed that Munz's *O. brachycarpa* actually consists of three allopatric species: *O. brachycarpa,* a diploid ($n = 7$) from western Texas to southeastern Arizona and northern Mexico; *O. howardii* (A. Nels.) W. L. Wagner, consisting of tetraploid, hexaploid, and octoploid plants ($n = 14, 21, 28$) from eastern Colorado, Utah, and eastern Nevada (Wagner, 1983); and *O. coryi,* described here, a tetraploid occurring from north-central Texas to the southern Texas Panhandle.

Oenothera coryi W. L. Wagner, sp. nov. TYPE: U.S.A. TEXAS: Taylor Co., eroded red clay soil, Camp Barkeley, 1 July 1943, *W. L. Tolstead 7537* (MO-1266818, holotype; BH 2 sheets, GH, MICH, NEB 2 sheets, NY 3 sheets, SMU, TEX, isotypes).

Oenothera brachycarpa var. *typica* sensu Munz (all material except the type), Amer. J. Bot. 17: 368. 1930, non Munz (as to the type).

Folia linearia ad angusto lanceolata margine integro vel in dimidio inferiore remote pinnatilobato; flores vix odori, petalis flavis mox dilute aurantis; capsula abrupte ad rostrum apicale producta, valva quaque ala marginali 4–6 mm lata praedita.

Acaulescent or caulescent and caespitose perennial herbs from a stout woody taproot with a usually branched caudex sometimes producing clusters of rosettes 10–60 cm across. Leaves linear to narrowly lanceolate, 5–16 cm long, (2–)3–5(–7) mm wide, densely strigillose, apex long-attenuate, acute to rounded, margin entire to the lower half remotely pinnately-lobed. Flowers 1–3, rarely more, opening near sunset, weakly scented. Buds with free sepal tips 0.7–1.2 mm long. Floral tube (5.5–)7.5–10(–12.5) cm long. Petals yellow, fading orange, drying lavender to purple, broadly obovate, 3.5–4.3 cm long, 3.7–4.2 cm wide, sometimes with a terminal tooth ca. 2 mm long. Capsule ovoid in outline, 2.5–3 cm long, usually abruptly constricted to an apical

[1] This material is based upon research supported by a grant to Peter H. Raven from the National Science Foundation.

[2] Department of Botany, Bernice P. Bishop Museum, P.O. Box 19000-A, Honolulu, Hawai'i 96817.

beak, each valve with a marginal wing 4–6 mm wide. Seeds in 2 distinct rows per locule, often reduced to one row near the apex, or occasionally only one row throughout, obovoid to subcuboid, angled, dark brown, 2.5–4 mm long, the surface corky and coarsely rugose to furrowed especially on the abaxial surface toward the proximal end, the distal end with a thick ridge on the abaxial and lateral sides of the seed; the testa very thick especially at the distal end, this area with a conspicuous internal cavity adjacent to the embryo. Self-incompatible. Mitotic chromosome number, $2n = 42$.

Distribution. Open grassland or disturbed areas such as roadcuts from Baylor, Knox, Throckmorton, Nolan, Taylor and Callahan counties in north-central Texas and Crosby and Garza counties in the Texas Panhandle, 350–920 m. Flowering in April and May.

Oenothera coryi is named in honor of V. L. Cory (1880–1964), who recognized this plant as a new species but never published it. This new species is equivalent to Munz's *Oenothera brachycarpa* var. *typica* (1930). The type of *O. brachycarpa* A. Gray [Pl. Wright. 1: 70. 1852. TYPE: Between present-day Val Verde and El Paso counties, Texas, July to November 1849, *C. Wright s.n.* (GH, lectotype, photo MO, TEX; US, isolectotype; Munz, Amer. J. Bot. 17: 368. 1930).] is not from west-central Texas as Munz thought, but, based on Charles Wright's itinerary for 1849 (McKelvey, 1955), it appears to have been collected in southwestern Texas between Val Verde and El Paso counties. Thus the plants from west-central Texas need a name. Apparently Munz, who did not know Wright's route at the time, placed the type specimen with others from west-central Texas because of its narrow leaves, although he commented (1930, p. 368) that the capsule wings of the type of *O. brachycarpa* were narrower than all other collections that he placed in his var. *typica*. Narrow wings are typical of *O. brachycarpa*. I am describing this entity endemic to west-central Texas as *Oenothera coryi*. Not only is its range completely separate from that of *O. howardii* to the north and west in Colorado, Utah, and Nevada, and that of *O. brachycarpa* to the south, in western Texas to southeastern Arizona and northern Mexico, but it is also morphologically distinct. *Oenothera howardii*, to which *O. coryi* is most closely related, can be distinguished by its consistently oblanceolate, elliptic, or sometimes lanceolate leaves, strongly scented flowers with a sweet odor, free sepal tips 1–3(–4) mm long in bud, plants usually at least sparsely hirsute, brilliant yellow and usually larger petals (3–)4–7.3 cm long that fade deep red and dry deep reddish purple or reddish brown, and its capsules that gradually taper to a sterile beak. *Oenothera brachycarpa* differs from *O. coryi* in its grayish green leaves usually with a terminal lobe, longer floral tube (9–)12–21(–22) cm long, longer free sepal tips 1–7 mm long, broadly rhombic-obovate petals, and presence of hirsute as well as strigillose pubescence.

OENOTHERA SECTS. *RAVENIA, EREMIA, CONTORTAE* AND *PACHYLOPHUS*

In the most recent evaluation of *Oenothera* subg. *Pachylophus* (Raven, 1970) eight species were included, *O. muelleri* Munz, *O. tubifera* Sér., *O. xylocarpa* Cov., *O. primiveris* A. Gray, *O. caespitosa* Nutt., *O. cavernae* Munz, *O. brandegeei* (Munz) Raven, and *O. macrosceles* A. Gray. In that paper these species were tentatively divided into four groups: *O. muelleri* and *O. tubifera* with white flowers and stout, obtusely angled, nontuberculate capsules; *O. xylocarpa* and *O. primiveris* with yellow flowers and stout, acutely angled, nontuberculate capsules; *O. caespitosa, O. cavernae,* and *O. brandegeei* with white flowers and stout, tuberculate capsules; and *O. macrosceles* with yellow flowers and slender, quadrangular, nontuberculate capsules. Raven (1970) suggested that these eight species were related and could be considered as constituting one somewhat heterogeneous subgenus or alternatively the four subgroups could be recognized as distinct sections.

Recent study of crossing relationships, vegetative, capsule, and seed morphology (Stubbe & Raven, 1979; Dietrich et al., 1985) suggests that *O. macrosceles* is best grouped with *O. maysillesii* Munz, *O. stubbei* Dietrich, Raven & W. L. Wagner, and *O. organensis* Munz in sect. *Oenothera* subsect. *Emersonia* (Munz) Dietrich, Raven & W. L. Wagner. The other species placed in subg. *Pachylophus* fall into four crossing groups whose members cannot be successfully hybridized with species of a different group (Wagner, unpubl.; Stubbe, unpubl.; Raven, 1970): 1) *O. muelleri* and *O. tubifera*; 2) *O. primiveris*; 3) *O. xylocarpa*; and 4) *O. caespitosa, O. brandegeei* and *O. cavernae* (Raven, 1970; Stockhouse, 1973; Wagner et al., 1985). Morphology, especially of

capsules and seeds, and a cladistic analysis support the four crossing groups (Wagner et al., 1985; Wagner, unpubl.). Anatomical evidence from a genus-wide study of seeds (Tobe et al., in press) showed that each of the crossing groups has distinctive anatomical features, although *O. xylocarpa* is very similar to *O. maysillesii* and *O. primiveris*. The *O. caespitosa* group and the *O. muelleri* group have conspicuous, unique, derived features. In view of the narrow sectional concept established by Lewis and Lewis (1955) for *Clarkia* and subsequently followed in all systematic studies of the family, these four groups of *Oenothera* should be recognized as sections. Three of the four sections are described here as new, and sect. *Pachylophus* is now delimited to include *O. caespitosa* and four related species (Wagner et al., 1985). Subgenus *Pachylophus* is no longer recognized. With these adjustments *Oenothera* is divided into 14 sections, each of which is composed of very closely related species that share numerous morphological features, anatomical features, and, based on crossing studies, similar genomes and usually similar plastomes. At present no subgenera are recognized, but work in progress (Wagner & Raven, unpubl.) summarizing all available data for the genus suggests that it may be possible to subdivide it into two subgenera.

I. **Oenothera** L. sect. **Ravenia** W. L. Wagner, sect. nov. TYPE: *Oenothera muelleri* Munz.

Oenothera subg. *Pachylophus* sensu Munz, Amer. J. Bot. 18: 728. 1931, pro parte; N. Amer. Fl. II. 5: 98. 1965, pro parte.
Oenothera subg. *Raimannia* sensu Munz, N. Amer. Fl. II. 5: 104. 1965, pro parte.

Plantae perennes hirsutae strigillosaeque vel subglabrae; tubus floralis recurvus; petala alba; capsula oblongo-lanceolata angulis acutis ad rotundatis; semina respectu morphologia saepe irregularia 3–7 mm longa supervicie adaxali costis longitudinalibus praedita.

Fleshy-leaved perennial herbs; stems several, arising from the rosette, decumbent to ascending. Pubescence of two types: hirsute, the hairs usually with a purple pustulate base and strigillose, the leaves sometimes glabrous. Buds curved downward by the recurved floral tube. Petals white. Capsules oblong-lanceoloid, somewhat curved, the angles acute to rounded, sessile. Seeds in 1 or 2 rows per locule, basically obovoid to oblong or oblanceoloid, often somewhat irregular, 3–7 mm long, the abaxial surface with longitudinal ribs; the testa very thick above the raphe and at the distal end, the thickened area with a cavity not visible externally or rarely appearing as a distal pore and/or a raphial groove. Self-incompatible (*O. muelleri*) or self-compatible (*O. tubifera*), outcrossing or modally autogamous, respectively. Basic chromosome number, $x = 7$.

The two species of this section, *Oenothera muelleri* and *O. tubifera,* have disjunct and presumably relictual ranges in Mexico from 2,300 to 2,500 m in Madrean woodland vegetation. *Oenothera muelleri* occurs in Nuevo Leon, Tamaulipas, and Coahuila, and *O. tubifera* occurs further south and west in the states of Hidalgo, Puebla, Guerrero, and Durango. This section appears to represent a lineage that diverged early in the evolution of the genus from ancestors similar to sect. *Oenothera* subsect. *Emersonia* (Raven, 1970; Stubbe & Raven, 1979; Wagner et al., 1985) and it is the sister group to sects. *Eremia, Contortae,* and *Pachylophus* (Raven, 1970; Wagner et al., 1985). The sectional name is intended to honor Peter H. Raven, who initiated this series of revisionary works on *Oenothera* over 25 years ago and who first placed the species of sect. *Ravenia* together as close relatives in 1970.

II. **Oenothera** L. sect. **Eremia** W. L. Wagner, sect. nov. TYPE: *Oenothera primiveris* A. Gray.

Oenothera subg. *Pachylophus* sensu Munz, Amer. J. Bot. 18: 728. 1931, pro parte; N. Amer. Fl. II. 5: 98. 1965, pro parte.

Plantae annuae hirsutae strigillosae et glanduloso-puberulae; tubus floralis recurvus; petala flava; capsula fere lanceolata ad ovoidea angulis acutis; semina obovoidea ad oblanceolata, 3–3.5 mm longa crasse rugosa, superficie adaxali sulco conspicuo area crassa cum forma U circumcincto.

Winter annual herbs, acaulescent or caulescent; stems when present usually simple, but occasionally with secondary branches arising from near the base, densely leafy, primary stem erect, secondary branches ascending. Pubescence of three types: hirsute, on the stems and ovary, the hairs usually with a reddish purple pustulate base; strigillose; and glandular puberulent. Buds curved downward by the recurved floral tube. Petals deep yellow. Capsule lanceoloid to ovoid, falcate or curved to nearly straight, the angle acute, sessile. Seeds in 2 rows per locule, obovoid to oblanceoloid, 3–3.5 mm long, coarsely rugose on the distal half of the abaxial side, the raphial face

with a conspicuous groove surrounded by a U-shaped, thickened area terminating at a pore near the distal end, the entire surface papillose, the papillae apically depressed; the testa very thick above the raphe and at the distal end, the thickened area with a cavity that appears as a pore near the distal end and a groove along the raphial face. Self-compatible, rarely self-incompatible, outcrossing to autogamous. Basic chromosome number, $x = 7$.

Oenothera primiveris, the only species of this section, is scattered or occasionally locally common in the Mojave, Sonoran, and Chihuahuan deserts, 30–1,600 m, in sandy soils in low desert to mountain foothills. Based on a cladistic analysis, especially utilizing seed morphology, sect. *Eremia* appears to be most closely related to sect. *Pachylophus* (Wagner et al., 1985), a relationship supported by the recent analysis of seed coat anatomy (Tobe et al., in press). The sectional name is the Greek word *eremia,* meaning desert, in reference to the restriction of this section to the North American deserts.

III. **Oenothera** L. sect. **Contortae** W. L. Wagner, sect. nov. TYPE: *Oenothera xylocarpa* Cov.

Oenothera subg. *Pachylophus* sensu Munz, Amer. J. Bot. 18: 728. 1931, pro parte; N. Amer. Fl. II. 5: 98. 1965, pro parte.

Plantae perennes brevi-hirsutae interdum sparse hirsutae; tubus floralis erectus; petala flava; capsula fere lanceolata angulis acutis tortuosis contortis pagina conspicue rugosa; semina grosse rugosa superficie adaxali cristis duabus parvis longitudinalibus praedita.

Acaulescent perennial herbs. Pubescence of two types: short-hirsute, the hairs erect to curved and somewhat appressed; occasionally also sparsely hirsute especially on floral parts. Buds erect. Petals bright yellow. Capsule lanceoloid, flexible, falcate, tapering gradually to a long slender sterile apex, the angles acute, contorted and twisted, the surface conspicuously wrinkled, sessile. Seeds in 1 row per locule, often becoming 2 rows toward the base of the capsule, obovoid, coarsely rugose, the surface with turgid and collapsed papillae, the raphial face with 2 small, longitudinal ridges nearly the length of the seed. Self-compatible, outcrossing. Basic chromosome number, $x = 7$.

The only species in sect. *Contortae, Oenothera xylocarpa,* is locally abundant from 2,250 to 3,050 m in open meadows, flat areas, or on slopes in loose granitic gravel, sand, or pumice. It grows in *Pinus jeffreyi* Balf. forest with *Artemisia tridentata* Nutt. or in *Pinus contorta* Dougl. ex Loud. subsp. *murrayana* (Balf.) Critchf. to *Abies magnifica* Andr. Murray forest and is known from three disjunct areas in California and adjacent Nevada: 1) Mount Rose, Washoe Co., Nevada, 2) southern Sierra Nevada, southwestern Mono Co., California, from the vicinity of Crestview south to Casa Diablo, and 3) southern Sierra Nevada, west-central Inyo and eastern Tulare counties, California, area bounded by Horseshoe and Big Whitney Meadows to the east and north, and Casa Vieja and Volcano Meadows to the south and west. The sectional name is derived from the Latin word *contortus,* twisted, in reference to the unique contorted capsules of *O. xylocarpa.*

Oenothera xylocarpa is here placed in a monotypic section because, like *O. primiveris,* most of its specialized features are not shared with any other species. Based on its lanceoloid, acutely angled capsules and relatively large seeds with papillose surface, it definitely appears to be part of the lineage that includes sects. *Ravenia, Eremia,* and *Pachylophus.* Hybrids cannot be formed in crosses with any of these species, although abortive seeds are sometimes formed in crosses between *O. xylocarpa* and *O. primiveris* or *O. maysillesii* (sect. *Oenothera* subsect. *Emersonia*). A recent study of seed anatomy (Tobe et al., in press) showed that the seeds of *O. xylocarpa* and *O. primiveris* differ from those of *O. maysillesii* primarily only in having thinner endotesta and irregularly swollen exotestal cells (papillose seed surface), but that *O. primiveris* differs further from the other two species in its thicker, 1 or 2 cell-layered exotegmen and thicker, 2–5-layered mesotesta. Cladistic analysis using general morphological characters and seed morphological characters suggests that *O. xylocarpa* probably diverged from these species relatively late in the evolution of the group and subsequently developed a number of unique derived features (Wagner et al., 1985).

OENOTHERA SECT. *LAVAUXIA*

Oenothera sect. *Lavauxia* is a distinctive section of five species. They are characterized by narrowly ovoid, ellipsoid to rhombic-obovoid capsules with oblong wings that extend essentially throughout the capsule body or triangular wings confined to the upper one-quarter to

two-thirds of the capsule. The seeds are asymmetrically cuneiform and the surface is minutely beaded. The collective range of the three North American species, *O. flava* (A. Nels.) Garrett, *O. triloba* Nutt., and *O. acutissima* W. L. Wagner, extends no further south than Guanajuato and Hidalgo, Mexico. The other two species, *O. centauriifolia* (Spach) Steud. and *O. acaulis* Cav., are disjunct in Argentina, Uruguay, and Chile. The two groups differ in features such as petal color and proportion of the capsule that is winged. The North American species have yellow petals and wings extending two-thirds or throughout the capsule length, whereas the South American species have white petals and wings extending only one-quarter to one-half the capsule length. The following subsection is proposed for the two South American species.

Oenothera L. sect. **Lavauxia** (Spach) Endl. subsect. **Australis**[3] W. L. Wagner & Dietrich, subsect. nov. TYPE: *Oenothera centauriifolia* (Spach) Steud.

Petala alba; plantae brevi-villosae; capsulae alae abrupte ad medium truncatae; intra medium carentes.

Petals white; plants short-villous, the hairs transparent to translucent, rarely creamy white, 0.1–0.4(–0.5) mm long, mixed with minute erect transparent glandular hairs, 0.1–0.2 mm long, and sparsely hirtellous, the hairs transparent to translucent, 0.7–1.7 mm long, these sometimes with a pale reddish purple pustulate base, only rarely strigillose with creamy white hairs 0.1–0.3 mm long; capsule wings abruptly truncated ⅓–½ of the way from the capsule apex, and absent or nearly so from the lower half of the capsule.

In addition to the new subsection of sect. *Lavauxia,* a nomenclatural change is needed for one of the North American taxa in this section. *Oenothera flava* occurs from Saskatchewan and Alberta, Canada, to western parts of the Great Plains, nearly throughout the Rocky Mountains to eastern Oregon and California, and south to the states of Guanajuato and Hidalgo, Mexico. Throughout most of its range it is modally autogamous, growing in seasonally moist sites or along streams; however, in montane areas of Arizona, New Mexico, and the Sierra Madre Occidental, Mexico, a large-flowered, modally outcrossing form replaces the autogamous plant. Previously these outcrossing plants had been considered a distinct species, *O. taraxacoides.* Careful study of these plants throughout their range (Wagner, unpubl.) showed that they intergrade extensively with *O. flava,* especially in Arizona near Flagstaff and throughout northern Mexico. Because of this intergradation and because it differs primarily only in flower size and breeding system, it is here treated as a subspecies of *O. flava.*

KEY TO THE SUBSPECIES OF *OENOTHERA FLAVA*

1a. Stigma elevated above or outside the ring of anthers; petals usually obcordate, (2.5–)3–4.5(–5) cm long; sepals often flecked with reddish purple splotches and with free sepal tips in bud (1.7–)2.5–10(–12) mm long; seeds over 2.5 mm long ..... subsp. *taraxacoides*

1b. Stigma surrounded by anthers; petals usually obovate with a terminal tooth, (0.7–)1–2.6(–3.8) cm long; sepals generally lacking reddish purple splotches and with free sepal tips 1–2(–5) mm long; seeds 1.8–2.2(–2.6) mm long ..... subsp. *flava*

Oenothera flava (A. Nels.) Garrett subsp. **taraxacoides** (Woot. & Standl.) W. L. Wagner, comb. et stat. nov. *Lavauxia taraxacoides* Woot. & Standl., Contr. U.S. Natl. Herb. 16: 155. 1913. TYPE: U.S.A. NEW MEXICO: Otero Co., James Canyon, Sacramento Mountains, 2,800 m, 6 July 1899, *E. O. Wooton s.n.* (US-563856, holotype, photo MO; POM, RM, isotypes). *Oenothera taraxacoides* (Woot. & Standl.) Munz, Amer. J. Bot. 17: 362. 1930.

Oenothera flava subsp. *taraxacoides* is colonial, rarely abundant in rocky clay- or sandy-loam soils of montane meadows to gravelly or sandy sites along seasonal or permanent watercourses in ponderosa pine, spruce-fir, or pine-oak forests, from three disjunct areas: 1) the Mogollon Plateau in Arizona to Catron Co., New Mexico; 2) Sacramento Mountains and Sierra Blanca, Lincoln and Otero counties, New Mexico; and 3) the Sierra Madre Occidental from northern Chihuahua south to Durango, Mexico.

[3] Treatment of this new subsection in collaboration with W. Dietrich, Botanisches Institut der Universität, Universitätsstrasse 1, D-4000, Düsseldorf 1, Germany.

LITERATURE CITED

DIETRICH, W., P. H. RAVEN & W. L. WAGNER. 1985. Revision of *Oenothera* sect. *Oenothera* subsect. *Emersonia* (Onagraceae). Syst. Bot. 10: 29–48.

LEWIS, H. & M. E. LEWIS. 1955. The genus *Clarkia*. Univ. Calif. Publ. Bot. 20: 241–392.

MCKELVEY, S. P. 1955. Botanical Exploration of the Trans-Mississippi West, 1790–1850. Arnold Arboretum, Jamaica Plains, Massachusetts.

MUNZ, P. A. 1930. Studies in Onagraceae V. The North American species of the subgenera *Lavauxia* and *Megapterium* of the genus *Oenothera*. Amer. J. Bot. 17: 358–370.

RAVEN, P. H. 1970. *Oenothera brandegeei* from Baja California, Mexico and a review of subgenus *Pachylophus* (Onagraceae). Madroño 20: 350–354.

STOCKHOUSE, R. E. 1973. Biosystematic Studies of *Oenothera* L. Subgenus *Pachylophus*. Ph.D. dissertation. Colorado State Univ., Fort Collins.

STUBBE, W. & P. H. RAVEN. 1979. A genetic contribution to the taxonomy of *Oenothera* sect. *Oenothera* (including subsects. *Euoenothera, Emersonia, Raimannia* and *Munzia*). Pl. Syst. Evol. 133: 39–59.

TOBE, H., W. L. WAGNER & H.-C. CHIN. 1986. A systematic and evolutionary study of *Oenothera* (Onagraceae): seed coat anatomy. Bot. Gaz. (Crawfordsville) (in press).

WAGNER, W. L. 1983. New species and combinations in the genus *Oenothera* (Onagraceae). Ann. Missouri Bot. Gard. 70: 194–196.

———, R. STOCKHOUSE & W. M. KLEIN. 1985. The systematics and evolution of the *Oenothera caespitosa* species complex (Onagraceae). Monogr. Syst. Bot., Missouri Bot. Gard. 12: 1–103.